African Invertebsrates Vol. 48 (2) Pages 245–251 Pietermaritzburg December, 2007

Permomerope natalensis sp. n. from the Lopingian of South Africa, and a redescription of the type species of *Permomerope* (Trichoptera: Protomeropidae)

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ABSTRACT

The trichopteran family Protomeropidae is recorded in South African deposits for the first time. A new species, *Permomerope natalensis* Sukatsheva & Mostovski, sp. n., is described from the Lopingian (Late Permian) of KwaZulu-Natal, South Africa. It differs from all previously known species in having a noticeably shorter CuA base, a much shorter MA_{3+4}, and in the absence of r–rs near the end of Sc. The type species of the genus, *P. australis*, is redescribed on the basis of a newly found specimen, and the generic diagnosis is amended. The wing venation of members of the family Protomeropidae is discussed. An identification key to four known species of *Permomerope* is provided.

KEY WORDS: Trichoptera, Protomeropina, Protomeropidae, *Permomerope*, caddisflies, Late Permian, Lopingian, Gondwana, new species, wing venation, identification key.

INTRODUCTION

The caddisflies represent a small order of holometabolous insects, with approximately 13 000 extant and about 650 extinct species. This is an ancient and phylogenetically important order, which is probably ancestral to lepidopterans. With their hair-covered wings, adult caddisflies superficially resemble moths. Aquatic caddisfly larvae inhabit different types of water bodies and build attached or portable cases or cocoons, using various materials (Ivanov & Sukatsheva 2002). The oldest caddisflies belong to the suborder Protomeropina, comprising families Protomeropidae, Microptysmatidae, Uraloptysmatidae, and Cladochoristidae. This suborder is known from the Permian to the Triassic of Europe (Obora, Czech Republic), northern European Russia (Soyana, Arkhangelsk Region; Tschekarda, the Middle Urals; Tikhie Gory, Tatarstan), Middle Asia (Madygen, Kyrgyzstan; Karaungir, Saur Mountain Ridge, Eastern Kazakhstan), Siberia (Sarbala, Kuznetsk Basin), Southern Mongolia (Bor-Tolgoy), Australia (Belmont, Ipswich), North America (Elmo, Kansas), and from South Africa, where Van Dijk and Geertsema (1999) reported an impression provisionally assigned to the family Cladochoristidae from the Mooi River locality in KwaZulu-Natal.

Protomeropidae were medium-sized insects strikingly resembling mecopterans, especially in the structure of their wings with numerous cross-veins. However, the arrangement of the anal veins forming a loop separates protomeropids from Mecoptera. Protomeropidae are widespread and abundant in most Permian localities, suggesting that they lived close to the places of burial. Nonetheless, the absence of fossils of their immatures indicates their terrestial or soil-dwelling life mode (Ivanov & Sukatsheva 2002).

Judging from their numerous fossils, protomeropids generally resembled neuropterans and scorpion flies in having a slender body and wings with abundant venation that are folded in a roof-like manner. Detailed morphological analysis of the wing and body structure supports an assumption that protomeropids were more similar to neuropterans and scorpion flies than to typical caddisflies. A number of plesiomorphies such as multi-branched Sc and R, numerous end forks of longitudinal veins, and the presence of a fork on CuA, unite ancient representatives of the above orders (Novokshonov 1997, 2004). Based on these characters, as well as on the long S-like base of CuA, the Protomeropidae are especially close to the family Kaltanidae O. Martynova, 1958 (Mecoptera).

The general pattern of protomeropid wing venation has some peculiarities compared to that of other caddisflies. The wings are homonomous; the costal space is wide and traversed by numerous cross-veins; Sc joins R before the pterostigmal area; RS originates within the second quarter of the wing; RS(+MA) and MP split dichotomously into four main branches that end in numerous forks; the M base is free but closely adjoins the R base; CuP is simple and short; 1A is short, 2A and 3A form loops that represent rudiments of terminal parts of 2A and 3A (Sukatsheva 1976). One hypothesis suggests that the anal loop of extant caddisflies helps to keep the wings folded (Rasnitsyn 1980) and ensures their tight closure, which prevents the body of the insect becoming wet when it is submerged during egg laying (Martynova 1957). Another hypothesis suggests that the loop facilitates overlapping of the fore- and hindwing margins during their downward movement even in the absence of a special coupling mechanism (Brodskiy & Ivanov 1983; Ivanov & Sukatsheva 2002). In summary, the wing venation of protomeropids (Sukatsheva 1976) follows the scheme developed for Neuroptera and Protomecoptera (Ponomarenko & Rasnitsyn 1974).

Permomerope australis (Protomeropidae) was described by Tillyard (1926) from the Late Permian (Lopingian) beds of the locality of Belmont in New South Wales, Australia, on the basis of the distal portion of a forewing. This species was later redescribed by Riek (1953), who involved some additional material. However, the basal portion of the wing remained unknown. Another specimen of *P. australis* was found in the Belmont insect bed in New South Wales, Australia, by the second author. It is represented by a well-preserved complete forewing, which prompts redescription of this species. The Belmont insect bed belongs to the Belmont Conglomerate Member of the Croudace Bay Formation, Booraloo Subgroup, Newcastle Coal Measures, and is widely distributed over the North Belmont region. The geological setting and palaeoenvironmental and palaeoecological reconstructions of the Belmont insect bed have been discussed in detail elsewhere (Beattie 2007). According to climatic reconstructions (Chumakov & Zharkov 2003), the Belmont locality was situated within the southern temperate-cold belt of high latitudes.

Permomerope natalensis sp. n. comes from the Late Permian (Lopingian) locality of Bulwer, which is situated in western KwaZulu-Natal. The exact level of the origin of the holotype of this new species is unknown. The stratigraphy and palaeoenvironment of this locality are discussed by Gastaldo *et al.* (2005). The floral assemblage here was dominated by *Glossopteris*, and the depositional environment has been reconstructed in the form of deep channels and point bar/lateral accretion. According to Chumakov and Zharkov (2003), this locality was situated within the southern temperate semiarid belt of middle latitudes.

The examined material, including the holotype of the newly described species, is housed in the collections of the Australian Museum, Sydney (AMS) and the Natal Museum, Pietermaritzburg (NMSA).

TAXONOMY

Suborder Protomeropina Tillyard, 1926

Family Protomeropidae Tillyard, 1926

Genus *Permomerope* Tillyard, 1926

Permomerope: Tillyard 1926: 275; Riek 1953: 56; Sukatsheva 1976: 96; Jell 2004: 96.

Type species: *P. australis* Tillyard, 1926 (Newcastle Coal Measures, Belmont, Australia; Lopingian), by original designation.

Diagnosis: Forewing. Costal space very broad: at level of MP bifuraction, broader than subcostal and radial spaces combined; abruptly narrowing towards wing apex. Sc rather short, with numerous simple branches, merging with long R at end of second third of wing length. Costal space beyond Sc tip with several terminal branches of R. Veins RS(+MA) and MP with 17–22 terminal branches; terminal forks vary in length, but generally short. MP comb-like, starts branching slightly proximad of RS(+MA) bifurcation; stem of MP long, almost as long as cell between M and CuA bases. CuA with long, robust, S-like base. CuP simple. Broad postanal space with several cross-veins.

Species included: In addition to the type species and the new species described below, *P. karaungirica* Sukatsheva, 1976 and *P. ramosa* Sukatsheva, 1976 from the Tatarian of Karaungir (Kazakhstan).

Remarks: Currently the family Protomeropidae comprises seven genera: *Permomerope* Tillyard, 1926 with three species from the Lopingian of Belmont (Australia) and the Tatarian of Karaungir (Kazakhstan), monotypic *Platychorista* Tillyard, 1926 from the Cisuralian of Elmo (North America), *Marimerobius* G. Zalessky, 1946 with two species from the Cisuralian of Tshekarda (the Urals, Russia), monotypic *Karaungira* Novokshonov & Sukatsheva, 1993 from the Tatarian of Karaungir, Kazakhstan, and *Pseudomerope* Kukalová-Peck & Willmann, 1990 with four species, monotypic *Pseudomeropella* Kukalová-Peck & Willmann, 1990, and monotypic *Stenomerope* Kukalová-Peck & Willmann, 1990, all from the Cisuralian of Obora, Czech Republic.

The new species resembles some neuropterans of the Permian family Permithonidae—especially those showing impoverished venation (like *Sauropsychops* Vilesov & Novokshonov, 1994 from the Tatarian of Eastern Kazakhstan)—in having a similar costal space, long Sc+R and a similar postanal space. The postanal space of those forms is also intersected by strong oblique cross-veins, but its anterior margin is not straightened. This similarity is supported by the previous assignment of the holotype of *P. natalensis* sp. n. to Neuroptera close to the genus *Permithone* (van Dijk & Geertsema 1999). The new genus can be differentiated from the neuropterans on the basis of the long sigmoid base of CuA, the absence of concentrated Sc+R veins around the pterostigma, and the straightened posterior margin of the postanal space.

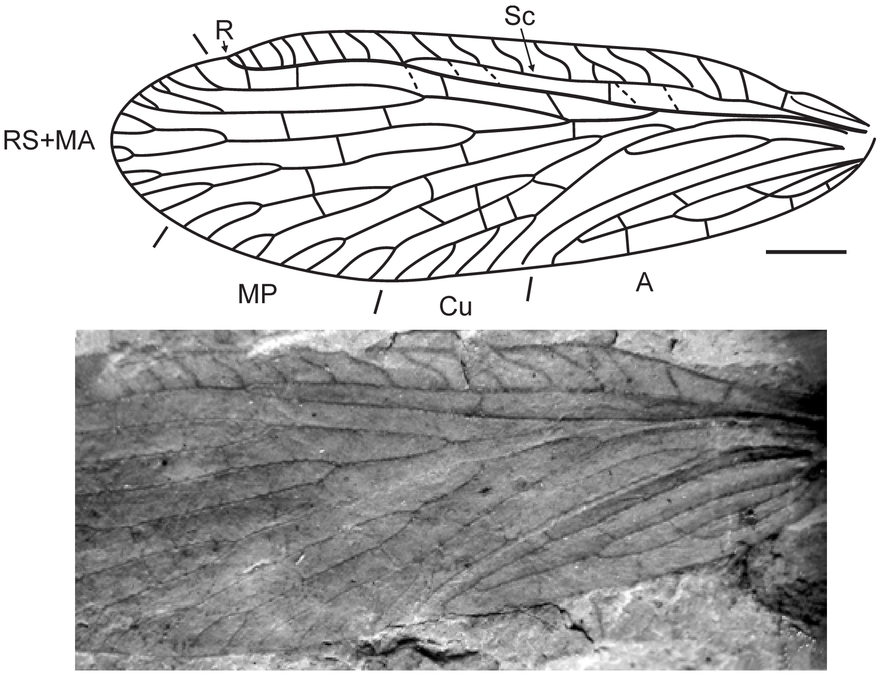

Fig. 1. *Permomerope australis* Tillyard, 1926, specimen AMF 130800, details of the wing venation and enlarged view of the basal half of the specimen. Scale bar = 1 mm.

Identification key to species of *Permomerope* based on forewings

1 CuA base shorter than RS stem, MA$_{3+4}$ clearly less than 2 times as long as MA, r–rs near Sc end absent .... **natalensis** sp. n.

– CuA base evidently longer than RS stem, MA$_{3+4}$ more than 2 times as long as MA, r–rs in vicinity of Sc end present 2

2 Sc terminates on R well distad of wing midlength, MA bifurcating distad of wing midlength, MP with less than 9 terminal branches .... **australis** Tillyard

– Sc terminates on R shortly after wing midlength, MA bifurcating prior to wing midlength, MP with more than 10 terminal branches 3

3 Cross-vein r–rs directly beneath Sc end, RS bifurcating prior to wing midlength, MP with 11 terminal branches .... **karaungirica** Sukatsheva

– Cross-vein r–rs slightly distad of Sc end, RS bifurcating distad of wing midlength, MP with 13 terminal branches .... **ramosa** Sukatsheva

Permomerope australis Tillyard, 1926

Fig. 1

P. australis: Tillyard 1926: 275, text-fig. 13; Riek 1953: 56, text-figs 1–3, pl. v (B), figs 6, 7; Sukatsheva 1976: 97 (key); Jell 2004: 96 (text-figs).

Redescription: Forewing 10.7 mm long and 3 mm wide, narrow, slightly broadened in its apical half, being broadest at the level of terminal branches of MP$_{3+4}$. Subcostal space with one distinct cross-vein. Sc weakly curved, with 7 or 8 long and oblique

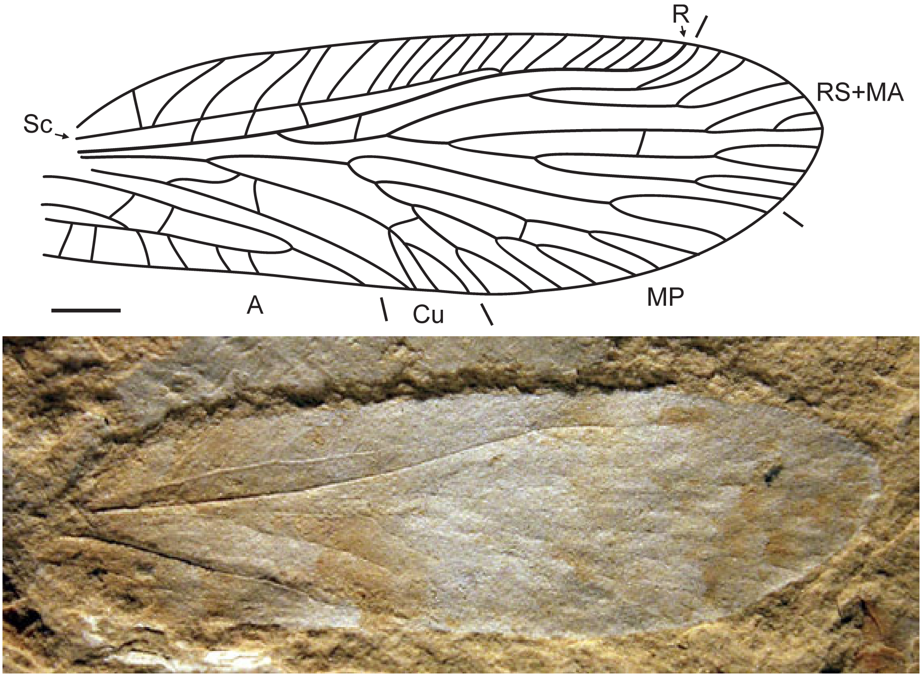

Fig. 2. *Permomerope natalensis* sp. n., holotype NMSA 2568a (counterpart), details of the wing venation and general appearance of the fossil. Scale bar = 1 mm.

branches. Pterostigma present. Sc+R arced towards anterior wing margin, with up to 6 veinlets in pterostigmal area. Veins RS(+MA) and MP with 18–22 terminal branches. RS stem as long as MA stem or slightly longer. MA_{3+4} 2.6 times as long as MA. RS_{1+2} 1.6 times as long as RS, with 4–6 terminal branches. Stem of M 0.8 times as long as RS. MP_{1+2} with 4 terminal branches, almost 3 times as long as MP_{3+4}, which ends in 4 branches. Distinct cross-veins developed between branches of RS, MA and MP. CuA 3- or 4-branched, with its base being more than 1.6 times as long as RS. 2A joins 1A not far from its end, 3A short; terminal section of anal veins subparallel to CuP. Postanal space with 4 oblique cross-veins.

Material examined: Holotype and specimens AMF 43119 (wing fragment), ANF 25208 (almost complete insect), AMF 130800 (complete wing). AUSTRALIA: *New South Wales*: Newcastle, North Belmont region; Lopingian, Newcastle Coal Measures, Booraloo Subgroup, Croudace Bay Formation, Belmont Conglomerate Member.

Permomerope natalensis Sukatsheva & Mostovski, sp. n.

Fig. 2

Etymology: The species name refers to the province of KwaZulu-Natal.

Description: Forewing 12 mm long and 3.7 mm wide, narrow (3.2 times as long as wide), weakly broadened in its apical half, being broadest at the level of terminal branches of MP_{3+4}. Subcostal space with three oblique cross-veins. Sc weakly curved, with more than 10 long and oblique branches. Pterostigma absent. Sc+R arced towards anterior wing margin, with 6 terminal branches. Veins RS(+MA) and MP with 20 terminal branches. Stem of RS almost 1.8 times as long as stem of MA. MA_{3+4} 1.4 times as long as MA. RS_{1+2} 1.3 times as long as RS, with 4 terminal branches. Stem of M 1.3 times as long as RS. MP_{1+2} with 2 terminal branches, almost 8 times as long as very short MP_{3+4}, which ends in 7 branches. Weak cross-veins developed between branches of RS, MA and MP. CuA 3-branched, with its base being noticeably shorter than RS. 2A joins 1A far from its end, 3A short; terminal section of anal veins subparallel to CuP. Postanal space with 6 oblique cross-veins.

Holotype: NMSA, no. 2568a/b, part and counterpart of complete, fairly well-preserved forewing, cross-veins may be partly invisible due to the state of preservation. SOUTH AFRICA: *KwaZulu-Natal*: Bulwer Quarry (29.79953°S:29.78657°E); Lopingian, Lower Beaufort Group, Normandien Formation (Balfour Formation equivalent).

Comparison: The new species differs from all previously known species in having a noticeably shorter CuA base, a much shorter MA_{3+4} (more than 2 times as long as MA in *P. australis*, 3 times as long as MA in *P. karaungirica*, and almost 4 times as long as MA in *P. ramosa*), and in the absence of r–rs near the end of Sc. Additionally, it differs from both *P. karaungirica* and *P. ramosa* in having a lesser number of MP branches (11 in *P. karaungirica* and 13 in *P. ramosa*).

ACKNOWLEDGEMENTS

The authors are most grateful to A.G. Ponomarenko, A.P. Rasnitsyn (both Paleontological Institute, Moscow) and V.D. Ivanov (St Petersburg State University) for their very useful comments on the manuscript, to D.E. Shcherbakov (Paleontological Institute, Moscow) for photographing the holotype of *P. natalensis* and discussions on the interpretation of the wing venation, to R. Jones and Yong Ye Zhen (AMS) for their help in photographing specimen AMF 130800, and to D. Vasilenko (Paleontological Institute, Moscow) for technical assistance. M. Mössmer (NMSA) is thanked for her professional editorial input. Sukacheva's study was supported by the Russian Foundation for Basic Research, grant no. 04-04-48296, and by the Presidium of the Russian Academy of Sciences Programme 'Origin and evolution of Biosphere, Subprogram II'. Beattie's study was funded by a Lake Macquarie City Council Grant, which was sponsored by Lake Macquarie City Council, Delta Electricity, Eraring Energy and Oceanic Coal, and grants from The Linnean Society of New South Wales and The Australian National University.

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